

IV.5 Environmental Factors That Affect Plant Quality

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Variation in host plant quality arises from many sources. Environmental stress, primarily a response to varying soil nutrients, light, and water, affects physiological responses by plants in a species-specific manner. This variation provides a remarkable array of available plant quality to insect herbivores (Coley et al. 1985, Chapin et al. 1987, Mooney et al. 1991). In addition, herbivore feeding (both insect and mammalian) further alters the nutritional quality of leaf material, both soon after feeding and in the future. Why do these responses occur? Plants reallocate minerals and energy in response to stress, and the consequence is considerable variation over time in the foliar concentrations of primary nutrients. These nutrients include levels of nitrogen-containing compounds, such as protein, energy-containing compounds, such as nonstructural carbohydrates (including free sugars), or specific chemical constituents, such as individual amino acids. Clearly, grasshoppers seldom face a simple “nutritional environment” when searching for food to satisfy crucial needs.

As variable plant quality often influences grasshopper population dynamics, can range managers predict how plant quality varies in time and space? For managers charged with long-term planning, which sites typically exhibit higher host plant quality? Will stress explain observed spatial patterns in plant growth and foliar quality? Will identification of stressed areas help identify grasshopper problem areas? Answers to how grasshopper food resources vary in time and space will provide important insights to aid in both forecasting grasshopper population change and formulating appropriate management strategies.

In this chapter, I briefly outline how environmental stress affects plant response at several levels. Once plant responses are recognized, managers can more effectively incorporate these responses into strategic plans, including forecasting models and economic assessments.

Plants are integrated units, and plant stress cannot be evaluated except in that context. Photosynthesis (light and carbon dioxide [CO₂] capture), which occurs in leaves and to a lesser extent in stems, is coupled with nutrient and water uptake through roots to provide all essential raw materials for plant growth, development,

and reproduction. As in animals, different plant tissues and organs contribute different functions, and a plant must balance the action of each to promote healthy, whole-plant function. Available resources fall short of the amount needed to facilitate all life activities, so plants are forced to allocate scarce resources (fig. IV.5–1). Significant tradeoffs exist because the plant cannot supply resources to all of its parts simultaneously, given the competition for resources in a limited environment. This scenario is the notion of “source–sink” relationships (Turgeon 1989). A *source* provides limited resources (roots provide the plant with nitrogen), and a *sink* gets first priority for use of limited resources (the leaf needs nitrogen for photosynthesis). Note the cyclical nature of the relationship. Some resources are obtained by the plant through absorption of nutrients through the roots, and energy-containing and structural compounds are produced by photosynthesis. The available nutrient pool obtained in this fashion is then allocated to those tissues housing the most critical metabolic activity at the time—the sink(s). As conditions change, new sinks develop, and the allocation patterns can be altered quickly.

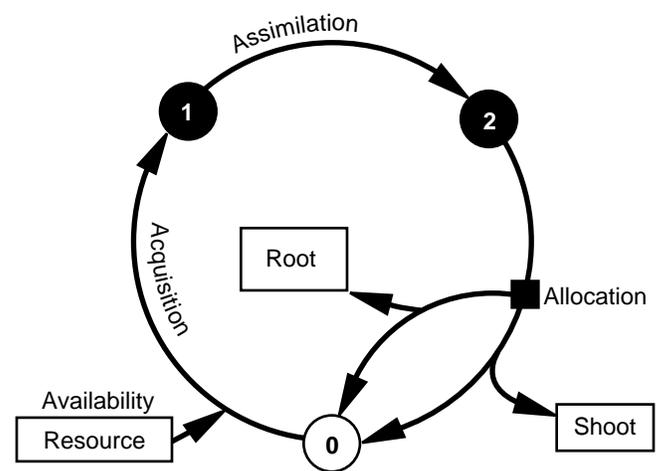


Figure IV.5–1—Simple, diagrammatic metabolic paths that indicate steps in obtaining and then allocating limiting resources among plant tissues. (Adapted from Sharpe and Rykiel 1991.)

Ultimately, these resource allocation “decisions” determine the fate of the whole plant in terms of survival, total biomass production, and long-term reproductive fitness. Because unlimited external resources seldom exist, plants cannot operate at maximal rates. The difference between optimal and actual rates of function defines the level of stress experienced by the plant (Mooney et al. 1991). As stress from such factors is imposed, it triggers a cascade of responses: the plant rebalances to the new conditions. Plants are exposed to a wide range of abiotic (weather) factors that directly reduce growth. These variable conditions include drought, flooding, mineral deficiencies or imbalances, temperature extremes, and air pollution (Jones and Coleman 1991). From the herbivore’s point of view, these cascading responses alter the nutritional quality and distribution in leaves.

As indicated in figure IV.5–2, Jones and Coleman (1991) provide an effective framework for quickly illustrating

both the types of plant responses to environmental stress as well as anticipated herbivore reactions to altered plant quality. Herbivory (livestock and insects) feeding on plants cannot be strictly separated from other stresses because losses in leaf, root, or stem material stress plants as much as physical or chemical factors.

Plant Responses

Both internal and external features control plant responses. Internally, individual genotypic differences and phenological development can exert significant effects on plant use and allocation of resources. For example, the plant genotype limits rates of acquisition, sets priorities for partitioning among plant parts, modifies allocation to biochemical processes, and determines the magnitude of other related responses, such as the amount of defensive compound that can be produced (examples in Jones and Coleman 1991).

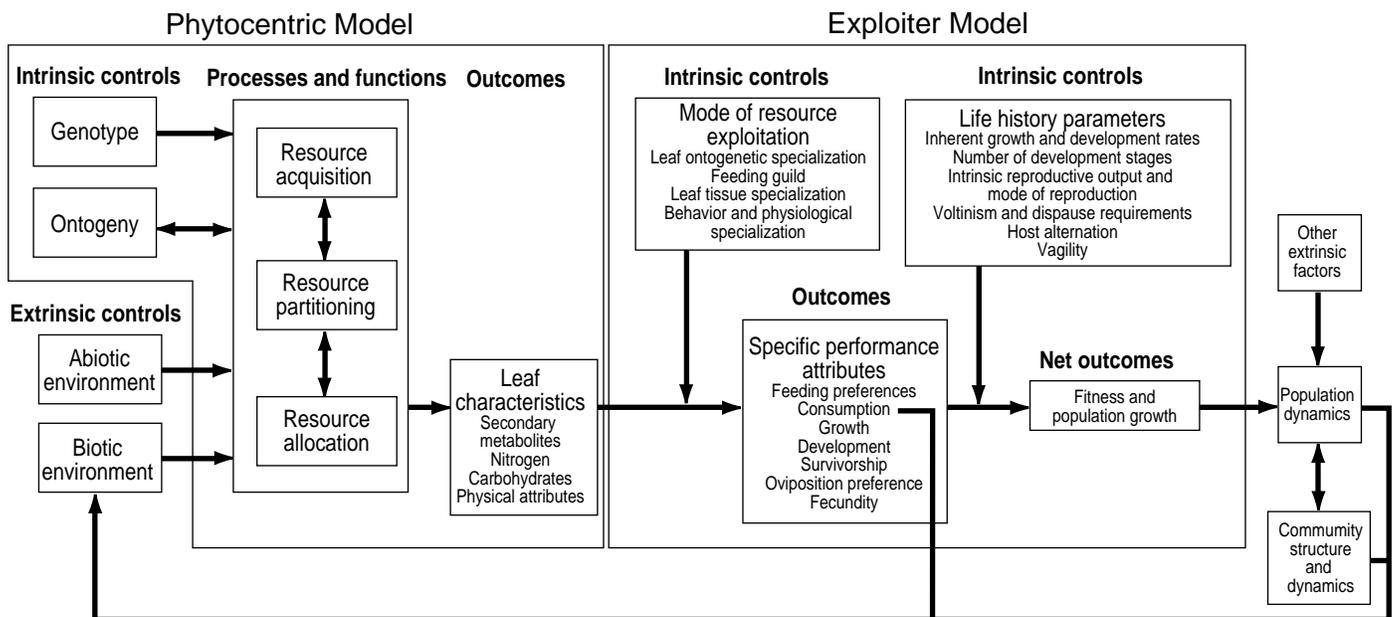


Figure IV.5–2—A conceptual framework of the linkages and feedbacks between plant allocation processes and herbivore consumers. (Adapted from Jones and Coleman 1991.)

Fast- versus slow-growing species typically exhibit very different patterns of nutrient allocation (Coley et al. 1985), largely due to the value of individual leaves. In fast growers, individual leaves are relatively less important than in slow-growing plants. Fast growers allocate a higher proportion of resources to growth and less to defense (chemicals and leaf structures that deter herbivory). The converse exists for slow-growing species. Seasonal plant growth modifies the capacity and demand for resources and sets partition and allocation priorities as plants grow and mature.

While intrinsic features clearly modify the strength of plant responses, external environmental features typically exert more influence on plant responses. Resources required by grasshoppers vary in both time and space; because some resources are limited, a plant is typically playing catchup. Within the limits imposed by genotype and phenological stage, plants attempt to obtain limited nutrients selectively. This process allows the plant to maintain a carbon-nutrient balance somewhere near the optimum for plant function. For example, plants limited by nutrients or water often allocate more resources to build root tissue to increase root surface area and increase nutrient absorption from the soil. As a result, leaf tissues receive fewer resources. The message here is that plants continuously respond to shifts in resource availability, resulting in significant changes in leaf quality.

In adjusting to variable resource availability, biochemical, anatomical, and physiological shifts also occur in the leaves. From an herbivore's point of view, both defensive secondary metabolites (described below) and nutritional features change. As stated earlier, the growth strategy of the plant (whether it is a fast or slow grower) dictates the response.

Secondary Metabolites.—Secondary metabolites in plants comprise a long list of compounds produced at various steps in the metabolic pathway that are not directly related to regulating photosynthesis or other primary metabolic pathways, such as respiration. So, while sucrose or enzymes are considered primary metabolites, a variety of chemical compounds such as alkaloids or phenolics are termed secondary. This term does not mean that these metabolites are unimportant for plant function or success—quite the contrary. According to Coley et al.

(1985), fast-growing plant species under stress should exhibit extensive variability in secondary metabolite production because growth is a higher priority than the production of defensive compounds. Conversely, allocation to secondary defensive compounds becomes a high priority in slow growers because leaf tissue must continuously be defended, even under stress. Finally, plant life form correlates well to the presence of and nature of plant defenses. Secondary metabolite defenses are much more common in forbs than grasses (Mole and Joern 1993, *contra* Redak 1987).

A diversity of chemical compounds serves to defend plants. In some plants, the defensive chemical also routinely serves a number of functions, while in other cases a plant uses different chemicals under different stress conditions (Coley et al. 1985, Jones and Coleman 1991). In addition, different forms of stress (drought, pollution, or nutrient deficiency) result in a diversity of responses as plant allocations vary with the stress. For example, drought responses are particularly complex. They alter acquisition of both carbon and nutrients, they disrupt transport function, and they cause secondary metabolite concentration to vary because water concentration in leaves varies.

Nitrogen.—Among all of the leaf nutritional characteristics that significantly respond to environmental stress and influence grasshoppers, nitrogen content is one of the most important. Many environmental stresses induce the mobilization of nitrogen in plants. This mobilization results in increased levels of total nitrogen as well as specific amino acids and proteins (Stewart and Larher 1980, Rhodes 1987). Drought and nutrient stress typically result in increased carbon-to-nitrogen ratios, often accompanied by altered amino acid composition (Stewart and Larher 1980, McQuate and Connor 1990), as shown in table V.5–1. Similarly, increased plant water stress (too little or too much water) often results in altered free amino acid composition. Free amino acids such as proline often increase in grasses with moderate water stress (Barnett and Naylor 1966, Hsiao 1973, Wisiol 1979, Bokhari and Trent 1985, Zuniga and Corcuera 1987), possibly because proline acts as an osmoregulator (Stewart and Lee 1974) or as storage for nitrogen and carbon (Barnett and Naylor 1966). [An osmoregulator serves to help maintain water balance within the plant.]

Table IV.5–1—Amino acids exhibiting increased concentrations in soybean leaves in response to increasingly severe water deficits (adapted from McQuate and Connor 1990)

Plant water deficit	Amino acids exhibiting increase
0 to –0.5 MPa ¹	Isoleucine, leucine, lysine, phenylalanine, tryptophan
–0.5 to –1.0 MPa	Cystine, glutamine, histidine, threonine, tyrosine, valine
–1.0 to –1.5 MPa	Proline
–1.5 to –2.0 MPa	Arginine, asparagine, glycine

Note: Reduction of leaf water potential is the decrease observed in water-deficient plants compared to well-watered individuals. Glutamic acid, alanine, aspartic acid, and serine do not change concentration in response to water deficit.

¹ Pressure units for plant water deficit are in megapascals (MPa).

Significant shifts in resource allocation often cause variation in many important nutritive chemicals. These chemicals include soluble nitrogen and free amino acids, nonstructural carbohydrates, and chemical defense molecules (Perry and Moser 1974, McKindrick et al. 1975, Chapin and Slack 1979, Mooney and Gulmon 1982, Bernays 1983). Total nonstructural carbohydrates (TNC) respond to environmental changes, such as grazing, temperature, water potential of soil and leaves, nutrient status of the soil, and maturity state of the plant (Ryle and Powell 1975, Bokhari 1978, Caldwell et al. 1981, Hayes 1985). Foliar carbon–nitrogen ratios can shift dramatically in response to grazing, water, and nitrogen fertilization (Bokhari 1978, Caldwell et al. 1981, Bryant et al. 1983, Mattson and Haack 1987).

Impact to Plant Quality From Biotic Sources

Interactions with herbivores, pathogens, and symbionts (organisms living in close association with the plant that confer a positive impact, such as nitrogen-fixing bacteria

in root nodules of many legumes) often significantly influence allocation schedules in plants, thus altering plant quality. In most North American grasslands, plants experience extraordinary pressure from cattle or sheep grazing, which severely reduces above- and belowground biomass. Thus, many range plants routinely suffer moderate to extreme stress from leaf loss from mammalian herbivores in addition to leaf losses from grasshoppers. In these cases, ecological interactions take place above versus below ground, mediated through the plant by changing allocation schedules.

Often, loss of either above- or belowground tissue alters the commitment to the other. For example, loss of leaf material from herbivores above ground results in reduced root mass. Root-grazing by a variety of nematodes and insect larvae leads to lower leaf mass above ground (Geiger and Servaites 1991, Mooney and Winner 1991). The soil surface effectively partitions the grazing system into these two components. Plants mediate interactions between aboveground versus belowground herbivores because herbivory in one compartment changes overall plant quality, often increasing herbivore load in the other compartment (Seastedt 1985, Seastedt et al. 1988). To range managers, management of plant loss in both compartments becomes critical because grazing pressure above ground can increase root quality to belowground feeders and thereby increase feeding on those tissues. Such complex responses further decreases the chance that plants will recover quickly from moderate to heavy grazing.

Such biotic interactions between plants and their herbivores are numerous. Some examples include mycorrhizal fungal or nitrogen-fixing bacterial associations with the roots, both of which increase nutrient acquisition rates by plants (Powell and Bagyaraj 1984, Arora 1991). Conversely, organisms causing plant diseases often lower rates of photosynthesis, respiration, and nutrient uptake as well as shift allocation schedules between roots and leaves, as do root-feeding nematodes (Ingham and Detling 1984).

In spite of significant grazing pressure, some plant species cope readily while others do not. Plants of different life forms (grasses versus forbs) typically differ in their tolerance to foliage loss. Plant life form influences

regrowth characteristics based on the protection or redundancy of primary growth tissue or the possession of such tissues that are typically missed by herbivores (Dahl and Hyder 1977). In grasses, the primary growing tissue is often found at the soil surface, below the level normally grazed by herbivores. In this sense, it is protected. Other adjustments that plants make to grazing include higher photosynthetic rates, reduced foliage longevity, low proportion of reproductive shoots, and faster rates of leaf replacement (Caldwell et al. 1981, Archer and Tieszen 1983). Species with the same life form (grasses), however, often can exhibit striking differences in response to herbivory.

How do grasses cope with herbivory? Caldwell et al. (1981) assessed physiological responses by two *Agropyron* bunchgrass species (*A. desertorum* and *A. spicatum*) that evolved with and without significant likelihood of herbivory. These grasses exhibited significant differences in tolerance to grazing, *A. desertorum* being more tolerant. Otherwise, these species exhibit similar growth timing and thus experience the same physical and climatic environment. Following grazing, *A. desertorum* rapidly established a new canopy with three to five times the photosynthetic surface than *A. spicatum* with the same available resources. *A. desertorum* exhibited a lower investment of nitrogen and biomass per unit of photosynthetic area, more tillers, more leaves per bunch, and shorter stems. In addition, this species exhibited greater flexibility of resource allocation following grazing by reallocating more resources to shoot growth at the expense of root growth. This process quickly achieved preclipping root–shoot balance. Nitrogen required for regrowth came from uptake rather than reserve depletion. Carbohydrate pools in the shoot system of both species remained low following severe defoliation. Interestingly, when competing plant species were removed, even the poorly coping *A. spicatum* could tolerate extreme defoliation (Mueggler 1972).

Final Comment

Take-home messages from these examples reinforce the major point of this section: resource allocation schedules for limited nutrients in plants largely dictate responses by mediating source–sink relationships. Consequently, any abiotic or biotic factor that alters these relationships will

change the allocation schedules, resulting in an altered nutritional environment for both mammalian grazers and insect herbivores, such as grasshoppers. An understanding of the general framework underlying source–sink and within-plant allocation provides the insight for anticipating favorable versus unfavorable conditions for both plants and herbivores. After all, range resource managers are really managing the vegetation resource, not the consumers per se. Such a realization will undoubtedly alter the way that humans devise strategies to manage grasshopper control programs.

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